Proceedings of the Iowa Academy of Science

Volume 71 | Annual Issue Article 14

1964

The Effect of Wind on Transpiration and Evaporation Through Multiperforate Septa

Irwin P. Ting
Iowa State University

Walter E. Loomis
Iowa State University

All cultures were examined for obvious aberrations of morphology of plasmodium and fruiting body, but none were noted. Sporangial size, capillitial and spore morphology, and stalk characteristics remained within average range.

Literature Cited

1. Gruen, H. E. 1959. Ann. Rev. Pl. Physiol. 10:405-440.
2. Alexopoulos, C. J. 1963. Bot. Rev. 29:1-78.
3. McManus, S. M. A. 1960. Nature 185(4705):44-45.
4. ------ and Kathleen Sullivan. 1960. Proc. Iowa Acad. Sci. 67:501-506.
5. ------ and S. M. S. Geraghty. 1962. Proc. Iowa Acad. Sci. 69:610-615.
6. Wittwer, S. H. and R. R. Dedolph. 1963. Am. Jour. Bot. 50:330-336.
7. Schaeffer, G. W., H. H. Smith and M. P. Perkus. 1963. Am. Jour. Bot. 50:766-771.

The Effect of Wind on Transpiration and Evaporation Through Multiperforate Septa[1]

IRWIN P. TING[2] AND WALTER E. LOOMIS

Abstract: Diffusion of water vapor through single-pore membranes with pores 100 to 800 μ in diameter and multipore membranes with pores 2.5 to 20 μ in diameter was studied as a function of wind velocity. The results of these studies are compared with data obtained with transpiring leaves in wind. It was found that wind had relatively little effect on small pores as compared with large pores and free water surfaces. The primary response of stomates or small, isolated pores to wind was simply an increase in the diffusion gradient. In general, the wind-to-still-air diffusion ratios determined with the use of small pores, either isolated or as a part of a multipore system, were less than 2, while the ratio for open surface evaporation in 1,000 feet per minute wind exceeded 15. The relatively small response of transpiration to wind is tenable, considering the epidermis as a multiperforate septum.

Considerations of the effect of wind on transpiration have varied from the work of Hygen (1), which indicated that wind increased stomatal transpiration, to the work of Manzoni and Puppo (2), which indicated that wind had no average effect. Martin and Clements (3) concluded that wind increased the rate of transpiration at low velocities but had relatively little additional effect at higher velocities. Martin (4) found that the ratio of transpiration in wind to that in still air averaged just over 2 for *Helianthus annus* under a variety of conditions. Huber (5), studying the effect of wind on small pore diffusion, concluded that the smaller the pore the less effect wind would have

[1] Journal Paper No. J-4858 of the Iowa Agricultural and Home Economics Experiment Station, Ames, Iowa. Project No. 1139.
[2] National Science Foundation Fellow

in increasing the diffusion rate. The purpose of this paper is to compare the response to wind of leaf surfaces and model systems composed of single-pore and multipore membranes.

Materials and Methods

Transpiration studies with potted plants were conducted in a plastic wind tunnel in the greenhouse. Transpiration was determined by weighing the pots to the nearest 0.01 g before and after the runs, which lasted from 15 to 30 minutes. The pots were covered with plastic bags to prevent evaporation from the pot and soil. Wind-to-still-air diffusion ratios were calculated from consecutive runs on a single plant. The stomatal condition at the end of each experiment was determined microscopically.

Model studies were made with single-pore membranes with pore diameters of 100, 200, 400, and 800 μ in brass stocks 50 μ thick and with a series of multipore membranes with 2,500 pores per cm^2 with pores 2.5, 5, 10, and 20 μ in diameter, made by the Buckbee Mears Co. of St. Paul, Minnesota. Diffusion trials were conducted by sealing the membranes with stopcock grease to small glass cups containing distilled water. In other tests, the membranes were placed directly upon wet filter paper. The wind trials were conducted on the laboratory bench under a glass wind tunnel. Wind was created by a table fan and measured with a hand anemometer. Diffusion was determined by weight loss from periodic weighings on an analytical balance. All tests were run in triplicate.

Table 1. Wind-to-still-air transpiration ratios obtained under greenhouse conditions

Species	Wind, ft/m	Light, ft-c	Stomatal[a] condition	Wind/[b] still
Cotton	390	1990	Open	1.53
Cotton	400	1980	Open	1.47
Cotton	420	1560	Open	0.69
Cotton	500	2400	Open	0.88
Cotton	520	910	Open	1.62
Cotton	590	1660	Slight closure	0.71*
Cotton	600	1600	Slight closure	0.32*
Corn	540	470	Closed ?	3.33
Corn	550	550	Closed ?	0.83
Corn	640	2150	Closed ?	2.88
Garden bean	630	800	Open	1.73
Garden bean	710	690	Open	1.54
Soybean	370	3590	Slight closure	0.90
Soybean	460	2860	Open	0.99
Soybean	480	2060	Open	1.84
Soybean	550	1610	Open	1.08

[a] Condition of stomates at end of trial as determined microscopically. The stomates of corn were never observed to be open.
[b] Ratios marked * were obtained with plants in dry soil.

Results

Table 1 lists the wind-to-still-air transpiration ratios obtained in the greenhouse. These data indicate that transpiration did not always increase in wind and that when an increase occurred, it was usually less than 2-fold. Decreases due to wind might be accounted for by reduction of leaf temperature (6) or stomatal closure. Microscopic observations did not, however, indicate significant stomatal closures in wind. To test the significance of wind on transpiration, the raw data were fitted to a multiple regression model. The individual plants were fitted to the model to eliminate variation. Other independent variables fitted to the model included wind, leaf temperatures, and light. The multiple regression coefficient for the data was 0.929, significant at the 99 per cent level. A *t*-test for wind was significant at the 95 per cent level despite the fact that a reduction in transpiration was obtained in several of the trials. Leaf temperature also was significant at the 95 per cent level, but light was not. Leaf temperature and wind were negatively correlated, indicating cooling of the leaves by the wind.

The diffusion through an isolated pore of stomatal dimensions varies directly with the diameter of the pore and can be adequately described by the equation,

$$Q = Ka, \qquad (1)$$

where Q is the diffusion, K is a constant including the gradient, and a is the diameter of the pore (7, 8). This equation will remain valid provided that the pore-tube length is not excessively great (9). Since it is the diffusion shells formed above and below the pore that cause diameter proportionality, wind by removing the shells may break the relationship. Noting that the diffusion can be described by the equation,

$$Q = Ka^n, \qquad (2)$$

where n equals one in the case of diameter proportionality and will approach two as the relationship shifts toward area proportionality, the effect of wind can be evaluated by taking the logarithm of each side to obtain the linear equation,

$$\log Q = n \log a + \log K. \qquad (3)$$

By plotting log Q against log a, the effect of wind (n) can be evaluated from the slope.

Table 2 presents data from several diffusion trials. Only high wind velocities showed significant changes in the diameter relationship. The maintenance of diameter proportionality in wind may be explained by protected diffusion shells below the membrane and possibly by small diffusion shells over the pores which are not destroyed by wind. By placing the membranes

directly upon wet filter paper, which reduced resistances to diffusion below the pores, a lower wind velocity (700 ft/m as compared to 1,000) broke diameter proportionality. It may be significant that values of n obtained by both experimental methods did not exceed 1.55. Jeffreys (10) in a theoretical consideration determined that the diffusion would vary with $a^{1.5}$ in a steady wind.

Table 2. Analysis of the effect of wind on small, isolated pore diffusion. The value of n represents the slope of the regression of log Q on log a. Values of one (1) indicate that the diffusion varied directly with the diameter of the pore. A value of two would represent area proportionality

Wind, ft/m	n (slope)[a]	Correlation[b] coefficient	Water source[c]
0	0.94	0.99**	Open surface
300	1.08	0.99**	Open surface
500	1.10	0.99**	Open surface
500	1.01	0.99**	Open surface
800	1.06	0.99**	Open surface
1,000	1.55*	0.99**	Open surface
0	1.09	0.99**	Filter paper
0	0.93	0.99**	Filter paper
200	1.03	0.99**	Filter paper
200	1.10	0.99**	Filter paper
550	1.15	0.99**	Filter paper
700	1.25*	0.99**	Filter paper

[a] Figures marked * are significantly different from one at the 95 per cent level.

[b] Correlation coefficients for the regression of log Q on log a.

[c] In the trials marked "Open surface" the water level was 1 cm below the membrane. In the trials marked "Filter paper" the membranes were placed directly on the filter paper.

The effect of wind on small pore diffusion is illustrated further by comparing the diffusion through single-pore and multipore membranes with the evaporation from a free water surface. Figure 1 is a plot of wind-to-still-air diffusion or evaporation ratios. The free water surface was an open cup with a diameter of 25,000 μ. Single-pores were of two sizes, 200 and 800 μ. The multipore membranes had pores 19 μ in diameter spaced at 10 diameters (190 μ) and thereby approximated an epidermis with with large stomates. A linear relationship between diffusion and wind velocity with the open surface and the smaller pore sizes was observed, while the larger 800 μ single-pore system showed an exponential function. Since in the multipore system during this trial, the water level was brought to within one mm of the membrane, is was assumed that limiting diffusion shells that may form between the water surface and the membrane were minimized, and the full effect of the wind should have been realized. The data indicate clearly that small pores do not respond to air currents as would be expected from a consideration of a free water surface. The response of the 200 μ system was nearly

identical to that of the multipore system, suggesting that the effect was due primarily to the size of the pores and not to the multipore system. The ratios of wind-to-still-air diffusion for the 19 μ multipore system were 1.12, 1.11, 1.44, and 1.66 for wind velocities of 200, 400, 700, and 1,000 ft./min. When it is considered that the evaporation from a leaf and the diffusion through multiperforate septa with pore dimensions and spacings comparable to stomates approaches free surface evaporation (9), the lack of agreement between multipore systems (leaf epidermis and multiperforate septa) and open surfaces in wind is important.

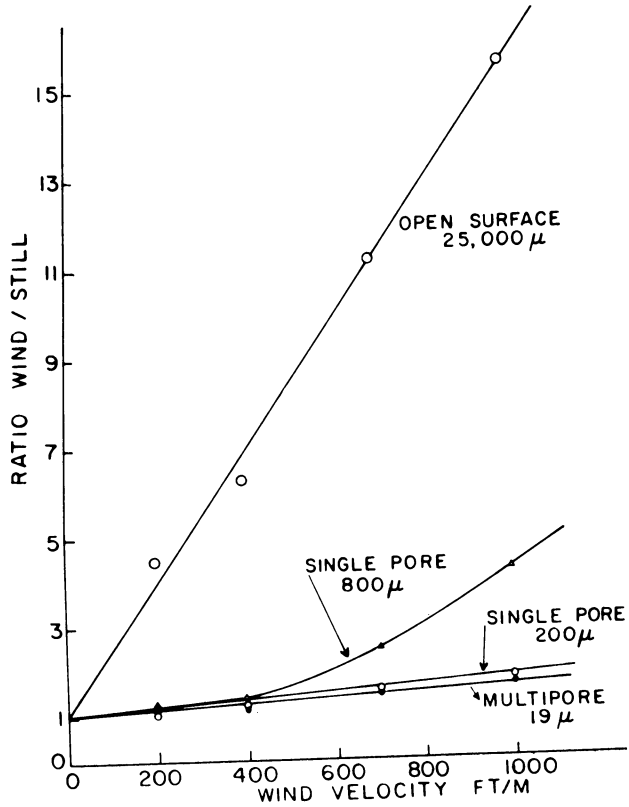

Figure 1. A comparison of the response of an open surface, single-pore, and multipore membranes to wind

There remains only a consideration of the effect of wind over the range of stomatal sizes. Figure 2 is a linear plot of diffusion through multipore membranes with pore diameters of 2.5, 5, 10, and 20 μ at three wind velocities. Since these membranes all had 2,500 pores per cm^2, they simulated stomatal opening or closing. It should be noted that the 20 μ points are from pores spaced at 10 diameters or 200 μ. A 50 per cent closure to a pore

diameter of 10 μ resulted in a relative spacing of 20 diameters, and the next two closures of 50 per cent gave pore spacings of 40 and 80 diameters. The latter spacings are in a range where no interference is expected (9). It is to be stressed that the sizes and spacings of the pores of these membranes are directly comparable to actual stomatal sizes. The 0 feet per minute curve depicts the change in diffusion which would be expected by stomatal opening or closing. The near linear portion of the curve at the smaller pore apertures is due to the wide relative spacing which results in no interference between the pores. As the pore size increased, interference increased, resulting in a very small change in diffusion with subsequent pore aperture changes. The general effect of wind was to increase the range of linearity that occurred at the smaller openings. This results from the removal of the vapor layer over the surface and, in part, from disruption of the micro-diffusion shells which account for the interference. The relative increases in diffusion were 1.14, 1.35, 1.47, and 1.46 for the 2.5, 5, 10, and 20 μ pores with a wind velocity of 350 feet per minute, and 1.42, 1.70, 1.89, and 1:88 for the same pores at a velocity of 600 feet per minute.

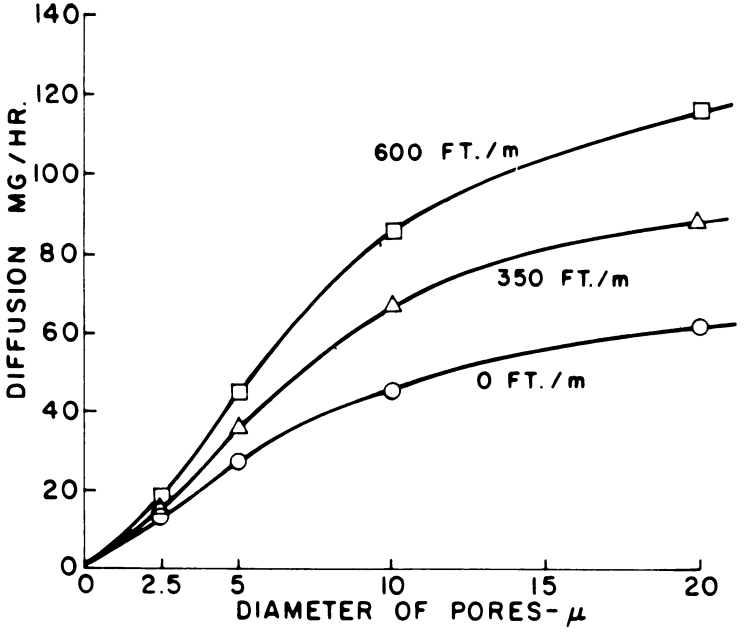

Figure 2. Effect of wind at three velocities on the diffusion through multipore membranes (The curves represent the changes expected in transpiration in still air and wind with stomatal opening or closing when the epidermis is considered solely as a multipore membrane)

Discussion

The major effect of wind on diffusion through small pores, either isolated or multiple, is to reduce the size of the external diffusion shells. The magnitude of the response will depend upon the size of the diffusion shells over the pores. Small pores, which necessarily are associated with small diffusion shells, respond only slightly to wind as compared with large pores and free water surfaces. Whether or not isolated pores differ basically from multipore systems in response to wind cannot be stated categorically. These experiments, however, do not indicate significant differences.

Since diffusion shells form on either side of the pores, and since only one diffusion shell appears to be necessary to maintain diameter proportionality, wind would not be expected to upset this general relationship except with large pores and high wind velocities. Under these conditions wind may not only remove the diffusion shells from the surface of the membrane, but also disrupt the lower diffusion shells by turbulence. The diffusion through small, isolated pores in wind can be described by

$$Q = K\, a\, f(w), \qquad (4)$$

where $f(w)$ is a function of the wind velocity. When wind reaches a critical velocity, which will be somewhat dependent upon a, the equation may tend to $a^{1.5}$, in accordance with Jeffrey's considerations (10).

Multipore diffusion is complicated by interference and a significant boundary layer of vapor, which decrease the expected diffusion per pore. By removing the boundary layer and disrupting the vapor shells, wind will tend to increase the diffusion rate; this, however, is in no way comparable to the response of an open surface.

The small response of transpiration to wind is tenable when the epidermis is considered solely as a multiperforate septum. The data of Woolley (11) indicated that such factors as ventilation, pumping, and decreased pressures on the lee side due to wind are relatively insignificant. Nothing has been said, however, of the effect of wind on leaf temperature. It can easily be shown that transpiration is nearly a linear function of leaf temperature; and wind, by its cooling effect (6), should tend to decrease the rate. Our transpiration studies in wind strongly suggest a leaf temperature-wind interaction. This interaction between the removal of vapor from the leaf surface by wind and the effect of altering leaf temperature is in need of further study.

Literature Cited

1. Hygen, G. 1954. Nytt Mag. Bot. 3:83-94.
2. Mazoni, L. and A. Puppo. 1943. Ricerche sulla transpirazione e sul

consumo idrico delle piante. Consiglio Nazionale Delle Ricerche Comitato Per L'Agricoltura. Anonima Arti Grafiche S. A. Bologna.
3. Martin, E. V. and F. E. Clements. 1935. Plant Physiol. 10:613-636.
4. Martin, E. 1943. Carnegie Inst. Wash. Publ. No. 550.
5. Huber, B. 1930. Zeitschr. Bot. 23:839-891.
6. Ansari, A. Q. and W. E. Loomis. 1959. Amer. Jour. Bot. 46:713-717.
7. Brown, H. J. and F. Escombe. 1900. Phil. Trans. Roy. Soc. London 193B:223-291.
8. Ting, I. P. and W. E. Loomis. 1963. Amer. Jour. Bot. 50:866-872.
9. Ting, I. P. 1964. Unpublished Ph.D. Thesis. Iowa State University, Ames, Iowa.
10. Jeffreys, H. 1918. Phil. Mag. 35:270-280.
11. Woolley, J. T. 1961. Plant Physiol. 36:112-114.

Extracellular Pectolytic and Cellulolytic Enzymes of *Pyrenochaeta terrestris*[1]

J. C. Horton[2]

Abstract. Extracellular pectolytic and cellulolytic ensymes were produced *in vitro* and *in vivo* by *Pyrenochaeta terrestris*. Mycelial development was sparse on cellulose, very good on glucose and best on pectin. Cellulase synthesis was the same at culture temperatures from 15°C to 30°C while pectinase synthesis was optimum at 20°C.

Pink root disease of onions incited by *Pyrenochaeta terrestris* (Hans.) Gorenz *et al.* occurs annually in all onion growing areas. Onion roots are commonly attacked late in the season, and disease progress is slow. Under certain conditions of water stress, disease progress may be rapid and loss severe (1). The ubiquity of the pathogen and the constant inoculum potential, despite long rotations, suggest a well adapted saprophytic phase (2).

In culture, however, the fungus competes poorly with other common soil inhabitants. Despite an extremely wide host range, involvements with root of other plants are very casual. Asexual spore structures are produced only sporadically, suggesting that the probable overwintering structure is mycelia. These apparent contradictions in behavior pose the interesting question of how this fungus survives for years at a high inoculum potential in the absence of onion hosts? Disease symptoms of root maceration and softening suggest that cell disrupting enzymes, such as cellulase and pectinase, may be involved pathogenically and also provide a means for saprophytic survival.

Materials and Methods

Isolates of *P. terrestris* (Table 1) were grown in standing cul-

[1] Journal Paper No. J-4895 of the Iowa Agricultural and Home Economics Experiment Station, Ames, Iowa. Project No. 1524.
[3] The following in 1.0 liter of solutiin: $NaNO_3$ 4.25 g, KCl 0.5 g NaH_2PO_4 1.4 g,